

THE MORPHOLOGY OF THE TADPOLE OF *XENOPUS LAEVIS*.

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(Read August 19, 1914.)

Material.—It was my intention to study the development in detail, but the Plathander (or, more correctly, Platanna), could not be got to oviposit in captivity and the tadpoles have been very scarce in ponds near Bloemfontein during the last two dry years. My youngest specimen should be about three years old, judging by particulars given by Leslie ; * for it has no tentacles, no tail fins, and its head is not yet flattened dorso-ventrally. I can accordingly say nothing about the early development.

Serial sections were prepared of five different stages, but as the head and branchial skeleton were considered of greatest importance, the series was not continued to the anus except in the youngest specimen. Two series ceased in the middle of the mesonephros and two were not taken beyond the head.

The Platanna tadpoles have been described and beautifully figured by F. E. Beddard,† and those points raised by him will first be discussed.

Sucker.—Beddard denies W. K. Parker's ‡ statement that a sucker is not developed ; I can support Beddard, for my youngest specimen has a distinct sucker.

Tentacles.—Boulenger, in a footnote to Leslie's already quoted paper, compares the tentacles of *Xenopus* to the balancers of Triton and Amblystoma ; Orr,§ according to Beddard, states that these balancers are the homologues of external gills belonging to the mandibular arch, and Beddard denies the homology of the tentacles and balancers, since the tentacles of the *Xenopus* tadpole are attached, on each side, to the

* Leslie, Proc. of the Zoo. Soc., London, 1890.

† Beddard, Proc. of the Zoo. Soc., London, 1894.

‡ Parker, Phil. Trans., vol. 166 (1877).

§ Orr, Q.J.M.S., 1889, p. 295.

"ethmoid just above the point where Meckel's cartilage articulates." It is of course clear that the tentacles cannot be mandibular gills if they are attached to the ethmoid; but a consideration of the clause in inverted commas shows, I think, that the word "ethmoid" is a mistake and must be replaced by "palatal portion of the palato-pterygo-quadrato bar" (see my Fig. 7 and the discussion on the first visceral bar). If such a substitution is made Beddard's objection falls to the ground. But I have found that not only is the tentacular cartilage joined "above the point where Meckel's cartilage articulates," but also to the ethmoid in front of the nasal sac, *i.e.* to the cornu trabeculae; and in view of this fact one must deny the homology of the *Xenopus* tentacles with the Triton balancers, unless one accepts the theory that the trabeculae cranii represent a pair of premandibular visceral bars. Beddard is of opinion that the tentacles should be compared to those of a Siluroid fish or "perhaps better to the nasal barbels of *Myxine* and *Bdellostoma*." The barbels of the Siluroids are supported by the rudimentary maxillaries, *i.e.* in the embryo probably by Meckel's cartilage. In *Myxine* the barbels are supported by cartilages which are figured free. In *Bdellostoma* the barbel-cartilages are attached to the lingual bar (*i.e.* either basi-hyal or basi-branchial). The homologies of the tentacular bars, as expressed by Beddard, are rather vague. I am of opinion that they represent labial cartilages, even although Beddard found that the posterior root was formed as an outgrowth from the ethmoid (palatal) cartilage.

Lungs.—Beddard observes that the high, columnar epithelium characteristic of the gill-slits does not extend into the glottis. My specimens, on the contrary, did show such an extension of the columnar epithelium, and therefore support the theory that the lungs and gill-slits are homologous organs (see Fig. 2, which is taken through the tadpole in a region posterior to the commencement of the groove leading to the third slit and still shows the tall epithelial cells medially; these extend backwards into the glottis).

Respiration.—Sedgwick* says that the larval respiration of *Aglossa* is entirely by means of lungs. Beddard states that since the filtering apparatus in the grooves leading to the gill-slits is the only observable respiratory organs, they must perform the act of respiration. Marshall and Bles,† as quoted by Beddard, say, for the Frog, "as the blood is returned from them (*i.e.* filtering apparatus) to the somatic veins, it is probable that they are not actively respiratory."

Beddard found external gills in the very young tadpoles, but did not know that they continued to be present at later stages, since he says that "they (filtering apparatus) clearly must be respiratory in *Xenopus*, as

* Sedgwick, "Student's Textbook of Zoology," 1905.

† Marshall and Bles, "Stud. Biol. Lab., Owens Coll.," ii., 1890.

there are no other gills." This is incorrect, as will be shown later under the heading "Operculum," but the gills cannot be respiratory, since they receive no special blood supply (see G1 and G2 of Fig. 5).

The lungs are developed and supplied with pulmonary arteries and veins at a very early stage, but they remain sacs with such delicate walls that it is not probable that they are the only organs active in respiration. Also, the tadpoles do come to the surface to swallow air occasionally, but they can remain under water for such long periods that the air cannot be their only source of oxygen.

The statement of Marshal and Bles that the blood from the filtering apparatus is drained into somatic veins, holds good also for *Xenopus*; for

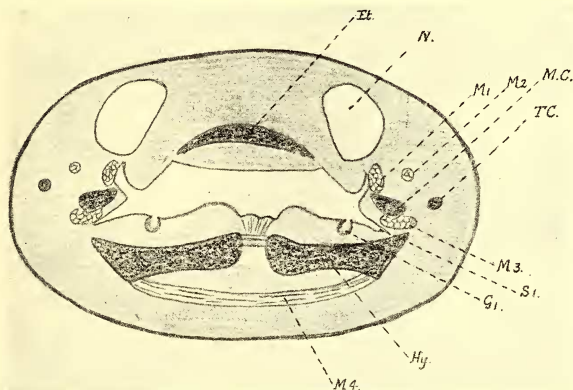


FIG. 1.—Et = Ethmoid cartilage; N = nasal sac; M₁ = muscle band attached anteriorly to dorsal edge of Meckel's cartilage, posteriorly to the hinder dorsal end of the pterygoid cart.; M₂ muscle band from M₁ to tentacle; MC Meckel's cart.; TC cart. from palatine to tentacle; M₃ muscle from outer edge of hyoid to Meckel's cart.; S₁ mandibulo-hyoid slit; G₁ thymus; Hy hyoid bar; M₄ "respiratory" muscle.

the lingual, external jugular and precaval veins (see Fig. 8) receive the blood from the three pharyngeal grooves, but I do not see why the respiratory function of these grooves should on this account be denied, especially when it is seen that they are so richly supplied with blood (A1-6 Fig. 7).

Gill-slits and Associated Glands.—Beddard noticed the deep pouch situated just behind Meckel's cartilage, and the lateral prolongations of this pouch represented, he thought, the mandibulo-hyoid cleft. Fig. 1 shows

these lateral prolongations as the slits, S1, and the small cup-shaped glands G1, associated with them.

The second gill-slit or hyo-branchial is shown in Fig. 3 as Sp between the hyoid bar (Hy) and the first branchial bar (Br); it does not open to the exterior. It has no gland associated with it.

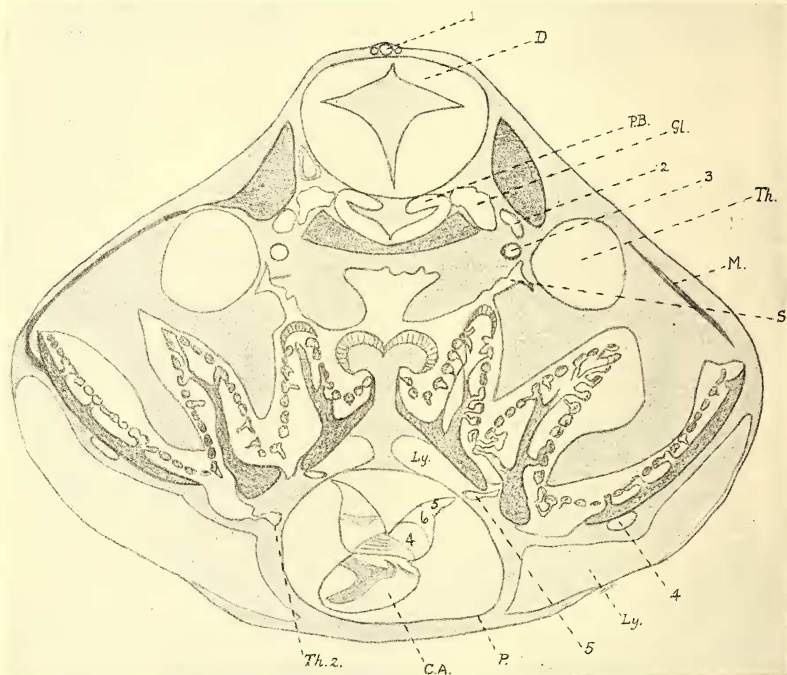


FIG 2.—1 backward continuation of anterior choroid plexus; D diencephalon; PB pituitary body; G1 ganglionar root of nerves 4-7; 2 internal jugular vein; 3 internal carotid artery; Th. thymus; M muscle joining 1st branchial bar to cranium (see opposite side of section); S see text; 4 systemic arch (3rd last); 5 2nd last aortic arch; 6 last aortic arch (pulmo-cutaneous); Ly lymph spaces; CA conus arteriosus; Th2 thymus.

The three branchial slits begin in the floor of the pharynx as grooves running obliquely backwards and opening through slits the anterior ends

of which are more ventral than the posterior. By these grooves the pharynx is widened in the manner shown by me* in a previous paper. In connection with the first branchial slit, apparently opening into the opercular cavity, but really situated near the base of the external gill of the second branchial bar (as I shall show later under the heading "Operculum"), there is another gland (G1 of Fig. 4 and Th2 of Fig. 2).

These two glands, the one in connection with the mandibulo-hyoid cleft (G1 Fig. 1) and the other in connection with the 1st branchial cleft (Th2, Fig. 2 and G1 Fig. 4), are no doubt thymus glands.

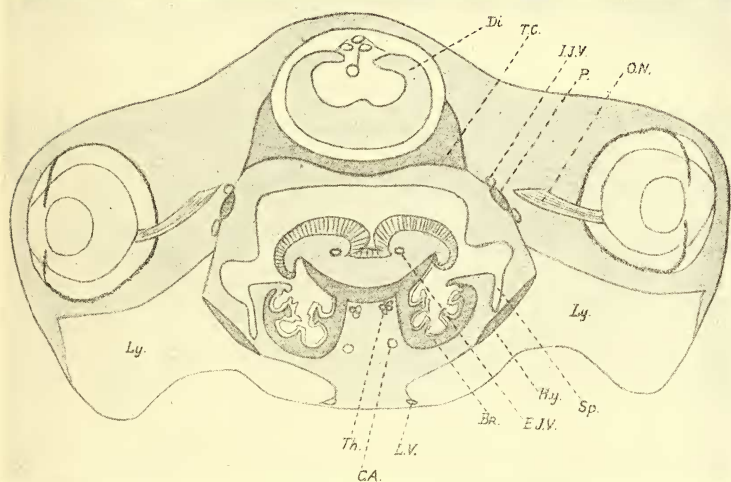


FIG. 3.—TC trabeculae cranii; IJV internal jugular vein; P palato-ptyergoid bar; ON optic nerve; Sp hyobranchial slit; Hy hyoid bar; EJV external jugular vein; Br 1st branchial bar attached to basi-branchial; LV lingual vein; CA carotid artery (external); Th thyroid gland; Ly lymph spaces.

The thyroid glands are present in the form of a pair of coiled tubules (Th of Fig. 3) which lie under the anterior connection, in front of I, Fig. 7, of the branchial bars to the basi-branchial. They do not open into the mouth in my youngest specimens.

In Fig. 5 of my previous paper, already quoted, there is shown two glands on the outer side of each external jugular (EJ); the anterior is

* Dreyer: *Trans. Royal Soc. of South Africa*, vol. iii., pt. 3, p. 353, 1913.

the thyroid, the posterior the thymus. It seems therefore that the anterior pair of thymus glands (those in connection with the mandibulo-hyoid cleft) do not develop in the adult.

Besides these glands there is another pair of glands (Th Fig. 2) which are much larger and are situated near the posterior end of a deep groove running between the palato-ptyergo-quadrate bar and the trabecula cranii; the groove commences just behind the palatal attachment of the bar and is continued backwards below the pedicel attachment. The groove S, as shown in Fig. 2, may appear to be adventitiously formed by the two flaps growing downwards into the pharyngeal grooves; further forwards, however [in Fig. 3 it has just "tailed out" in the edge of the

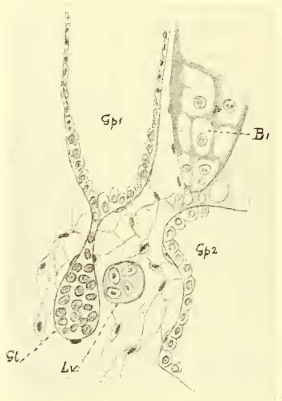


FIG. 4.—Lv = external jugular vein; B₁ = 1st branchial bar; G1 thymus gland; Gp₁ and Gp₂ 1st and 2nd external gill pouches.

pharynx pointing in a direction between the pterygoid (p) and the trabecula (TC)] it can be seen to be a perfectly well-defined groove which is probably the vestige of a premandibular gill-slit. The almost spherical, ductless, compact gland produced as a proliferation of the epithelium of such a slit could then also be called "thymus" gland. Now what I take to be the thymus glands of the adult are two yellowish, fatty-looking bodies situated in the floor of the mouth just behind the thyroid glands (the latter still recognizable as a pair of coiled tubules), *i.e.* exactly in the situations of the thymus glands of the 1st branchial slit. But the dorsal glands, *i.e.* those in connection with the "trabeculo-mandibular" slit would have a

position such as that defined for the thymus by Sedgwick (p. 277), viz. "close to the angle of the lower jaw (in the Anura behind the tympanic cavity and beneath the depressor mandibulæ muscle)". I take it, therefore, that it is these "trabeculo-mandibular" thymus glands which are developed in Anura. In *Xenopus*, although relatively enormous in the tadpole, they have escaped my notice in the adult.

Operculum.—The operculum on each side of the body is a ventro-laterally attached fold of skin which is broad in the middle and gradually tails out towards the posterior. Towards the anterior it becomes very narrow, and then its free anterior end is fused with the body-wall (Fig. 5,

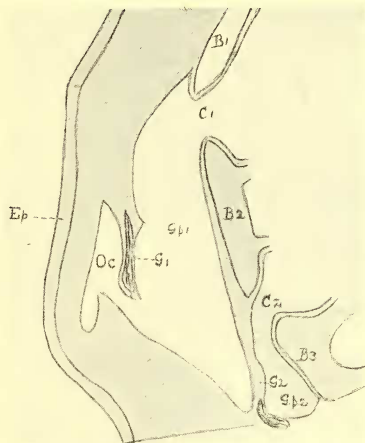


FIG. 5.—B1, 2, and 3 1st, 2nd, and 3rd branchial bars; C1 and 2 1st and 2nd gill slits; G1 and 2 1st and 2nd external gills; Gp1 and 2 1st and 2nd external gill pouches; Ep epidermis; Oc opercular cavity.

OC). It is a theory, generally accepted I think, that the operculum represents an external gill growing backwards from the hyoid bar. Fig. 5 shows that it only starts on a level with the beginning of the 2nd gill-slit and the end of the 1st gill-slit; reference to Fig. 7 will show that this is far back from the hinder ends of hyoid. However, if the hyoid were continued straight backwards it would lie directly under the attachment of the operculum so that, also in *Xenopus*, the two lateral opercula may be taken to be hyoidean gills.

The structure of each opercular cavity may be described as follows: There is firstly an outer groove formed by the upwardly bent opercular fold—this is the real opercular cavity, although only at the anterior end may it be called a “cavity.” Secondly, into this groove there open three pouches which I have called “external gill-pouches (Fig. 5, Gp 1 and 2). These three external gill-pouches may be imagined to have arisen by the partial fusion of the outer ends of three backwardly directed external gills—the last would of course fuse with the body-wall. Beddard actually saw external gills in very young tadpoles, and Fig. 5 shows two of these, G1 and G2. A section taken just in front of that represented by Fig. 5 would show the first gill, G1, attached ventrally, *i.e.* distally—it would be seen in the same way as is G2 in Fig. 5. The third gill commences further

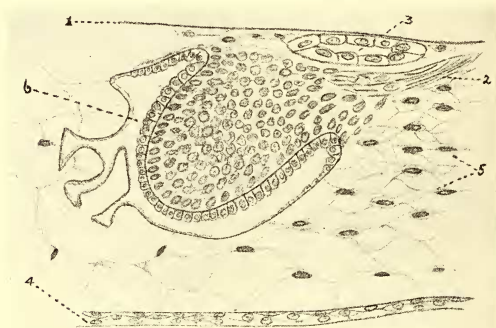


FIG. 6.—1 coelomic epithelium; 3 hinder end of pronephros; 2 nerve to arm; 5 connective tissue; 4 epidermis; 6 sac into which arm is invaginated.

back than the level of Fig. 5 and is attached to the third visceral bar (B3). Each external gill-pouch is provided with a band of muscle fibres (two are shown in the two gills in Fig. 5) which runs around it and is attached to the branchial bars in front of and behind it. The contraction of these muscles would put the contents of the pouches under pressure and at the same time widen the opercular openings of the pouches. The wall of the external gill-pouches, *i.e.* the gills, are not vascular, and cannot therefore be actively respiratory.

Fore-limbs.—The operculum, on each side, tails out just ventral to the end of the last branchial bar, while the fore-limbs are developed further backwards and, moreover, dorsal to the ends of these bars. The fore-limbs

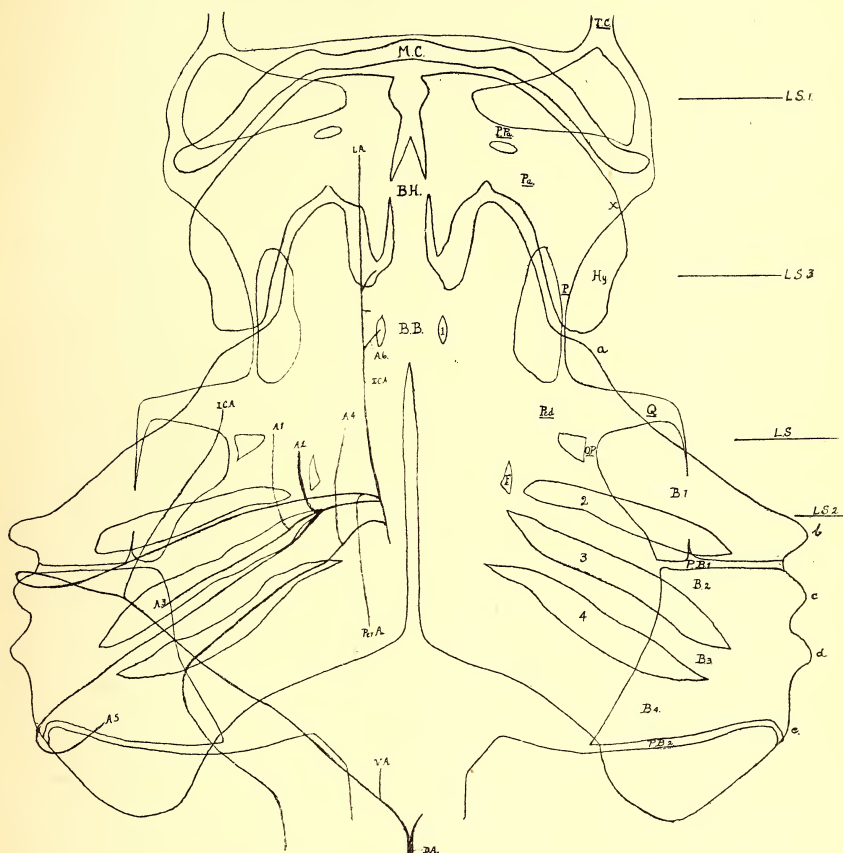


FIG. 7.—Reconstruction of cranium and visceral skeleton. On left side the arteries are put in schematically as thin lines. ICA = internal carotid artery; PerA = pericardial artery; DA = dorsal aorta; VA = vertebral artery; ECA = external carotid artery; Ped = pedicel of sub-ocular arcade; OP = otic process of subocular arcade; LS 1-3 = level of sections 1, 2, and 3. For rest of lettering see text.

are not, however, developed as simple outgrowths, but have what may be called an "endogenous" origin. Each arm is seen to lie in a little sac

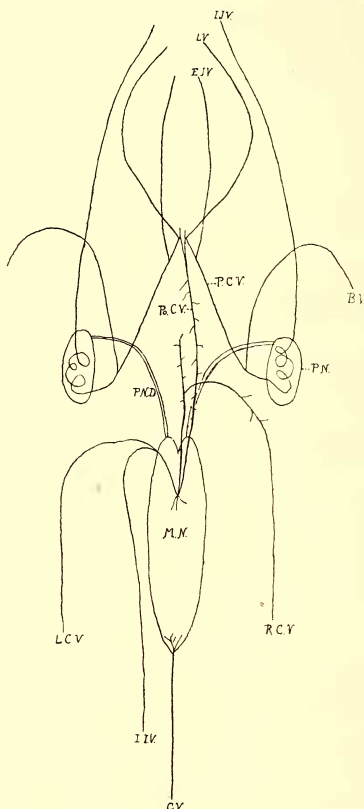


FIG. 8.—Schematic representation of the principal veins of the *Xenopus* tadpole (the pulmonary veins are omitted) from reconstructions of serial sections. PN = pronephros; PND = pronephric duct; MN = mesonephros. For rest of lettering see text.

(Fig. 6), but my material was not young enough to determine whether this sac was formed as an independent invagination or as a separation

from the end of the opercular cavity; its position is against the latter view.

Lachrymal Canal.—In more advanced tadpoles there is on each side a canal which, at one end, opens into the nasal sac just beside the external opening of the latter; from here it runs backwards and outwards, opening to the exterior by a double pore just above the articulation of Meckel's cartilage, behind the attachment of the tentacular bar. Its position, running from the nose to a region in front of the eye, and its double aperture suggests its homology with the lachrymal canal of reptiles, birds, and mammals; but it cannot be described as a duct running between the trabeculae and the palato-ptyergo-quadrate bar as the lachrymal duct should, according to Foster and Balfour.* Perhaps it is to be compared to the second nasal opening of Ganoids and Teleosteans.

Visceral Skeleton.—I have already mentioned the skeletal rods of the tentacles and expressed the opinion that they are homologous with labial cartilages (TC of Figs. 6 and 7).

First Bar.—The palatal portion is stout and is divided into two portions by a small foramen. The two portions may perhaps be the prepalatine cartilage (PPa) and the palatine (Pa). The articulation of Meckel's cartilage is far forward, but the pedicel (Ped) has also a large outward projection (Q), and I am of opinion that the latter (Q), and not the larval articulation, is the quadrate cartilage of the adult. Reasons for such an opinion are:—

1. The statement, common to textbooks, that during metamorphosis the quadrate articulation shifts backwards cannot be taken literally since then the palatines, which are necessarily the regions of growth for such a shift, would have to be directed obliquely backwards in the adult; instead, the palatines always point directly outwards.

2. The position of the pterygoid portion (P) would be shifted relatively to the palatine and quadrate unless the articulation *gradually* shifted back along it; but the change is rapid and could be much better explained by saying that the old articulation is retained; that during the late larval life Meckel's cartilage grows back past the articulation until it forms another articulation with (Q) on the pedicel; that during metamorphosis the larval articulation (with the palatine) is lost and the larger gape thus formed.

3. A figure by Milne Marshal, reproduced in Selenka ("Zoologisches Taschenbuch") for *Rana*, indicates as the quadrate a knob of cartilage behind the articulation of Meckel's cartilage.

4. The cartilage (Q) is connected distally with a plate of imperfectly chondrified connective tissue which may be regarded as the precursor of the cartilaginous ring around the middle ear of the adult.

* Foster and Balfour, "Elements of Embryology," p. 248.

5. If (Q) is the quadrate, *i.e.* if Meckel's cartilage only secondarily comes to articulate with the adult quadrate, then the common view that the mandibular bar becomes bent in the form of a $\succ$ to form the upper and lower jaws does not exactly express the facts of the case; for on this view the palatine cartilage is the most dorsal portion, the quadrate the ventral portion, of the upper segment. If my view is the correct one, then the palatine, which is the original articulation for Meckel's cartilage, must be ventral to the quadrate. I am thus going against accepted ideas in accepting an original palatal and secondary quadrate articulation of Meckel's cartilage; and these accepted ideas are so well supported by the structure of *Selachii*, *Batoidei*, and embryonic stages of higher groups that opposite views must be treated with caution. But if the "posterior lateral" cartilages of *Petromyzon* and the "coronal" cartilages of *Bdellostoma* should prove to be homologues of Meckel's cartilage, then my view would receive strong support, since these are admittedly most primitive groups. Also the structure of the jaws of the *Holocephalan*, *Chimaera* (with anterior, *i.e.* palatal, articulation of Meckel's cartilage) supports my view that the formation of the jaws is not simply a bending of the mandibular arch in the form of a $\succ$; that the posterior articulation of the lower jaw is secondary.

Second Bar.—In the *Xenopus* tadpole there is no indication that the hyoid has any part in the formation of the stapodial portion of the columella auris. The two hyoid bars are joined to a basi-hyal (BH Fig. 7) which is continuous with a basi-branchial (BB Fig. 7). At their outer edges the two hyoids are firmly attached by ligaments to the palatines at points (x Fig. 7) just posterior to the articulations of Meckel's cartilages. The outer edges of the hyoids are also joined by a stout plate of muscle fibres (Fig. 1 MH), and the contraction of these would cause the hyoid bars to bend upwards at their inner ends so that the mouth cavity would be reduced. If the mouth be filled with water, then closed and the "hyoid" muscle contracted the water would be forced through the pharynx; the hyoid bar is thus probably important for the processes of nutrition and respiration.

Branchial Bars.—The branchial skeleton consists of two plates joined to a median basi-branchial (BB). Each plate has four apertures, and the fact that there is an artery in connection with each of these may induce one to believe that there are really five branchial bars. Such an opinion would be strengthened by an inspection of the outline of the branchial plate which clearly shows five projections, *a*, *b*, *c*, *d*, and *e*, alternating with the apertures 1, 2, 3, and 4. Against the presence of five instead of four branchial bars, the following points may be raised:—

1. There are only three internal pharyngeal grooves, the first one

running forwards to the anterior edge of the supposed first bar from the supposed second.

2. The first aperture may also be explained as a vestige of the separation between the bases of branchials 2 and 3. The arrangement of the pouches—one starting in front, one behind, and one at it—would favour such a view. The artery passing through this aperture must then be regarded as a “new” development.

3. In other amphibia there are at most four bars—not five.

Thus, although at first sight there seems to be five bars, I have come to the decision that there are really only four.

With regard to the question as to the origin of the columella—the branchial bars are joined dorsally to the auditory capsule by a sheet of dense connective tissue in which there are several centres of chondrification, and there are also in this sheet two distinct bars of cartilage (PB 1 and 2), one attached to the auditory capsule just above the fenestra ovalis, the other joined to the extreme posterior region of the capsule. It seems unlikely that the first of these bars (PB 1), which is exactly in the position that the columella will later on be in, should totally disappear and be replaced by an upgrowth of the hyoid. It seems more probable that it is retained, and forms at least the stapedial portion of the columella. The two cartilaginous rods (PB 1 and 2) are, as mentioned above part of a continuous sheet of dense connective tissue, which in some places shows distinct chondrification and which stretches from the outer edge of the branchial plate to the auditory capsule and forwards to the quadrate (Q). Such a plate can only be considered to be the fused pharyngo-branchial elements of the branchial bars, and the stapedial portion of the columella is therefore probably of branchial and not of hyoidean origin.

BLOOD VASCULAR SYSTEM.

Venous System.—From the anterior part of the body the blood drains into the sinus venosus through three pairs of veins. The lingual vein (Fig 8 Lv) runs from the muscle (M4 Fig. 1) down to the skin (Lv Fig. 3). The external jugular vein (EJv Fig. 8) comes from the floor of the mouth (EJv Fig. 3). The precaval vein (pcv Fig. 8) comes from the pronephros through which it is continuous with an internal jugular vein (IJv Figs. 8 and 3; 2 Fig. 2). The internal jugular vein in the region shown in Fig. 2 gives off a branch which passes between the gland Th and slit S, and receives branches from the roof of the pharynx. The internal jugular also receives a number of branches from the brain and dorsal body-wall. The precaval just after leaving the pronephros receives a vein (Bv Fig. 8) from the outer edge of the filtering apparatus. The

(internal) pharyngeal grooves are thus drained by the external jugular and the precaval veins.

The anterior veins are thus the same in the tadpole as in the adult, but I now find that the labelling of Fig. 5 of my previous paper (already quoted) is incorrect; the veins EJ should be lingual, IJ should be external jugular, and SS internal jugular; the brachial and cutaneous of the adult are new developments.

There are pulmonary veins opening together, but apart from the other veins, into the imperfectly divided auricle at a very early stage of development.

There are no cuvierian ducts in the sense of ducts into which both precavals and postcavals open. The blood from the tail is carried by a single caudal vein (CaV Fig. 8) to the meso-nephridia; in the latter it breaks up into smaller vessels which unite again anteriorly to form the postcaval vein. The homologies of the posterior veins of vertebrates are still very obscure, and although it is, as a rule, undesirable to build a theory on observations on a single species, yet in view of the absence of any generally accepted theory another view-point cannot but be welcome. Bridge* splits up the original sub-intestinal vein into a postanal portion (the caudal vein), a posthepatic portion (the internal intestinal of Elasmobranchs: the anterior abdominal of Dipnoids: the hepatic portal of Teleosteans), and the prehepatic portion (the hepatic veins with sinus venous and auricle). The posterior cardinal veins Bridge takes to be a new development.

That the caudal vein is not a portion of the original sub-intestinal should, I think, be disproved by the following considerations:—

1. In the lowest forms such as *Amphioxus* it cannot be a median backward prolongation of the sub-intestinal, for the anus would be in the way.

2. Bridge apparently supports his view on the structure of the highly specialized Teleosteans (see his diagram, p. 322), whereas in the Elasmobranchs which, as he says, "exhibit a more primitive condition of the venous system in certain features than is the case in any other group," there is no connection between the caudal vein and the internal intestinal. Neither is there such a connection in Dipnoids.

3. Teleostean embryos have the caudal vein joined to the precavals.

Neither is it certain that the internal intestinal or anterior abdominal represents the posthepatic portion of the sub-intestinal for the relation of the postcaval to the posterior cardinals and to the internal intestinal is not quite clear. In Elasmobranchs the posterior cardinals are joined posteriorly in a way to suggest a postcaval; in Teleosteans only the one posterior cardinal suggests a postcaval; and in Dipnoi the similarity of

* Bridge, "Cambridge Natural History," Fishes.

one of the posterior cardinals to a post-caval is still more marked. Further, in *Amphioxus* the sub-intestinal vein is really a plexus of blood-vessels; in *Myxinidae* the portal continuation of the internal intestinal receives "the genital vein and some veins from the anterior part of the body" (Sedgwick); "in different Teleostomi it may also receive the veins from the pyloric cæca, from a portion of the air-bladder, the gonads, and, as previously mentioned, a tributary from the caudal vein" (Bridge). Various veins, which usually open into the posterior cardinals, may therefore open into the hepatic portals, *i.e.* into a portion of the sub-intestinal.

Taking these facts into consideration, I cannot but express the belief that the posterior cardinals are not (as Bridge assumes) "new" formations, but represent, together with the internal intestinal and hepatic portal, the sub-intestinal plexus of *Amphioxus*. The caudal should be a new development.

In the *Xenopus* tadpole the sub-intestinal plexus is represented by the following vessels:—

1. A vein running from the posterior end of the abdomen, through the intestines, from which it receives numerous branches, and opening into the postcaval immediately after the latter leaves the mesonephros. It probably represents the internal intestinal of fishes, and since it drains the same organs as does the anterior abdominal of the adult (rectum and small intestine) it will probably later on become attached to the ventral body-wall, develop somatopleuric veins in connection therewith, and so become the anterior abdominal.

2. Two dorso-lateral splanchnopleuric veins, one opening into the internal intestinal, the other into the hepatic portal; these cannot represent the lateral veins of fishes since the latter are somatopleuric; their attachments are against their being regarded as posterior cardinals, but if the sub-intestinal is taken to be a plexus, then the points of attachment of particular veins would not matter very much (consider, *e.g.* the various attachments of the spermatic veins in fishes), and we may consider these two veins as the homologues of the posterior cardinals of fishes. The one opening into the hepatic portal can be clearly recognized in the adult (Sp Fig. 5, Dreyer, already quoted) for in both it passes through the pancreas. That the other represents the mesenteric of the adult (Mes Fig. 5, Dreyer), is not certain, but is nevertheless probable, since in both cases there are only three posterior splanchnopleuric veins in connection with the hepatic portal.

3. On leaving the kidney the postcaval divides into two, both branches going to the right side of the body into the liver, the one branch remains on the dorsal aspect of the liver, receives numerous hepatic veins, passes in almost a straight line to the sinus venosus, and represents the

postcaval of the adult; the other curves round the liver and breaks up into numerous hepatic portal capillaries after receiving the right posterior cardinal. The tadpole thus differs from the adult in having the hepatic portal connected with the postcaval.

Arterial System.—Reference to Fig. 7 will show that there are vestiges of four arches: one passing upwards between the hyoid and the first branchial bars and three associated with the three gill-slits. Another, apparently aortic, arch passes through the slit I, but, as already mentioned, this slit cannot be held to be a gill-slit. The three internal gill-pouches are supplied with blood by all the arches except the second, *i.e.* the systemic, and the arrangement of the arteries to these pouches seem to have no significance, for A6 goes to the second pouch; A1, A2 first to the second then on to the first; A3 to the second; A4 and A5 to the third. Anyway, it will be seen that the internal gill-pouches are very copiously supplied with blood, so that we may consider them as important if not the sole respiratory organs.

Of the four arches only the second is connected to the dorsal aorta; but also the third, in younger individuals, would most probably have such a connection through A5.

The Nervous System.—The following cranial nerves were found:—

1. The olfactory, branching to the olfactory sacs and to Jacobsohn's organ.

2. The optic, to the eye. Anteriorly the pituitary body is continued as a laterally expanded, hollow, ventral outgrowth from the diencephalon; the optic nerve from each side is joined to this outgrowth on the same side, so that there is no crossing of the optic fibres to form a chiasma.

3. The oculomotor, leaving the brain just behind the pituitary body, receives a branch from the trochlearis as it leaves the cranium and goes to eye muscles.

4. Just in front of the auditory capsule there is a large ganglion which is joined (?) to the diencephalon just in front of the optic lobes. Distally the ganglion is continued into the following seven nerves:—

(a) The trochlearis, with a branch to the oculomotor and another to the muscles of the eye.

(b) The trigeminus: (a) one branch along the ventral surface of the pterygoid and into the muscle which joins Meckel's cartilage to the palatine portion of the palato-ptyergo-quadrate bar; (β) another branch to the epithelium of the roof of the mouth.

(c) The abducens, running along the dorsal surface of the pterygoid just ventral to the internal jugular vein and going to a ventral eye muscle.

(d) The facial, with the following branches: (a) running over the large

thymus (?) gland, along the outer, ventral surface of the eye to the skin ; (β) to the skin behind the eye ; (γ) to the skin above the brain and dorsal to the eye.

5. The otic ganglion with several nerves to the membranous labyrinth is joined to the dorsal surface of the ventricle just behind the optic lobes.

6. Small dorsal and ventral roots swell into a large ganglion just behind the auditory capsule. This ganglion gives off two nerves :

(a) The glossopharyngeal, giving off (α) a branch which runs along the bar (PB2 Fig. 7) and goes to the pharyngeal grooves ; (β) one running forwards dorsally to the thymus (?) gland and into the quadrate (Q Fig. 7) cartilage ; (γ) one running ventrally to the thymus (?) gland and the quadrate cartilage, along the dorsal surface of the pterygoid cartilage and into the muscles joining Meckel's cartilage to the palatine cartilage.

(b) The vagus with branches to the oesophagus and lung.

It will be noticed that although all ten nerves are developed they are joined to the brain by only six roots, which seems to indicate that the nerves are not outgrowths from the brain. This is, however, *en passant*, for only earlier stages than mine could decide such a question.

Each spinal nerve also ends in an endo-vertebral ganglion, the small upward prolongation of which is closely applied to the latero-dorsal surface of the spinal cord, it being impossible to say definitely whether it is continuous with the cord or not, although I am of opinion that it is not.

Except the vagus, I could find no nerves going to the splanchnopleure, so that the sympathetic cords must be developed late in the tadpole life (only two of my series were continued back far enough and stained suitably for the study of the spinal nerves).

RÉSUMÉ.

1. The tentacular cartilages are joined both to the ethmoid and to the palatal portion of the sub-ocular arcade.

2. The high epithelium of the gill-slits is continued into the glottis—in support of the theory that lungs and gill-slits are homologous.

3. The operculum encloses three external gills which are fused distally to form three external gill-pouches.

4. There are trabeculo-mandibular, mandibular-hyoid, and 1st-2nd branchial thymus glands.

5. In older tadpoles there are "lachrymal" (?) canals.

6. The anteriorly situated articulation of Meckel's cartilage is discussed.

7. There are two "pharyngo-branchials," one of which probably forms the stapedia portion of the columella auris.

8. The homology of the postcaval and posterior cardinals is discussed; the hepatic portal is joined to the postcaval at the point where the latter leaves the mesonephros. There are no cuvierian ducts.

9. The filtering apparatus is copiously supplied with blood from all the aortic arches except the systemic, and is probably the most important respiratory organ.

10. All the cranial nerves were found, but the 4th, 5th, 6th, and 7th were all united proximally to a single ganglion, which was joined (?) to the diencephalon in front of the optic lobes. The 9th and 10th were also joined in a single ganglion, perhaps attached to the ventricle.